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Soil enzyme activities during the 2011 Texas record drought/heat wave and implications to biogeochemical cycling and organic matter dynamics☆

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ABSTRACT

Extreme droughts and heat waves due to climate change may have permanent consequences on soil quality and functioning in agroecosystems. During November 2010 to August 2011, the Southern High Plains (SHP) region of Texas, U.S., a large cotton producing area, received only 39.6 mm of precipitation (vs. the historical avg. of 373 mm) and experienced the hottest summer since record keeping began in 1911. Several enzyme activities (EAs) important in biogeochemical cycling were evaluated in two soils (a loam and a sandy loam at 0–10 cm) with a management history of monoculture (continuous cotton) or rotation (cotton and sorghum or millet). Samplings occurred under the most extreme drought and heat conditions (July 2011), after precipitation resulted in a reduction in a drought severity index (March 2012), and 12 months after the initial sampling (July 2012; loam only). Eight out of ten EAs, were significantly higher in July 2011 compared to March 2012 for some combinations of soil type and management history. Among these eight EAs, enzymes key to C (β-glucosidase, β-glucosaminidase) and P cycling (phosphodiesterase, acid and alkaline phosphatases) were significantly higher (19–79%) in July 2011 than in March 2012 for both management histories regardless of the soil type ($P > 0.05$). When comparing all sampling times, the activities of alkaline phosphatase, aspartase and urease (rotation only) showed this trend: July 2011 > March 2012 > July 2012. Activities of phosphodiesterase, acid phosphatase, α-galactosidase, β-glucosidase and β-glucosaminidase were higher in July 2011 than July 2012 in at least one of the two management histories. Total C was reduced significantly from July 2011 to March 2012 in the rotation for both soils. Only the activities of arylsulfatase (avg. 36%) and asparaginase showed an increase from July 2011 to March 2012 for both soil types, which may indicate they have a different origin/location than the other enzymes. EAs continued to be a fingerprint of the soil management history (i.e., higher EAs in the rotation than in monoculture) during the drought/heat wave. This study provided some of the first evidence of the adverse effects of a natural, extreme drought and heat wave on soil quality in agroecosystems as indicated by EAs involved in biogeochemical cycling.

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1. Introduction

Drought and heat waves are expected to become more frequent and extreme due to global climate change for many regions (IPCC, 2007). The Southwestern U.S. is especially vulnerable, with drought frequency expected to increase significantly during the next century (Overpeck and Udall, 2010; Strzepek et al., 2010). Although periods of high temperatures and low precipitation are common in Texas, the period from October 2010 through September 2011 was the warmest and driest 12-month period on record (Hoerling et al., 2012). The average temperature in Texas for June through August 2011 was 30.4 °C, which was 2.9 °C above the long-term average and warmer than any previous single month. This record-breaking heat was accompanied by extreme drought conditions, with a drought index (i.e., Palmer drought severity index, PDSI) reaching a record minimum in September 2011 (Hoerling et al., 2012). In the Southern High Plains (SHP) of Northwest Texas, a leading region for U.S. cotton production, drought was so severe that almost all dryland crops were abandoned and irrigated crop

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yields were severely reduced with overtaxed wells not providing sufficient water to meet exceptionally high demand. While crop losses and record decline in groundwater supplies (HPWD, 2012) are clear impacts of the 2011 Texas drought and record heat, little is known about other less obvious consequences on ecosystem services related to biogeochemical cycling and soil organic matter (SOM) dynamics.

Enzyme activities (EAs) are critical to ecosystem functioning affecting nutrient transformation, carbon (C) sequestration and biogeochemical cycling of C, nitrogen (N), phosphorous (P) and sulfur (S). The activities of enzymes have been used as sensitive indicators of soil quality changes as affected by management and land uses in soils from humid and semiarid regions (Bandick and Dick, 1999; Ndiaye et al., 2000; Acosta-Martínez et al., 2003, 2004a,b). In the SHP region, increases up to 37% has been found in EAs after only 2–3 rotations of sorghum with cotton (Acosta-Martínez et al., 2011) and within two years following conversion from monoculture cotton to high input forage sorghum cropping systems without a change in soil organic C (Cotton et al., 2013). However, little is known about how these ecosensors respond to drought and whether soil type (e.g., differing textures) or management history affects the response under natural conditions in the field as most studies on the effects of drought and warming on soil EAs are conducted under simulated conditions (i.e., Sardans and Peñuelas, 2005; Bell et al., 2009). Under simulated drought conditions, soil EAs have shown a decrease as soil moisture is gradually reduced in native ecosystems in which other dynamics are involved (i.e., changes in plant physiology and biomass) (Sardans and Peñuelas, 2005; Sardans et al., 2008a,b). Warming alone has not shown consistent effects in EAs on different simulated studies, with no change to slight increases depending on other factors, i.e., season and climate (Bell et al., 2010; Steinweg et al., 2013). The majority of climate change research has concentrated on natural ecosystems (i.e., forests or grasslands) while studies on extreme weather conditions are lacking in agroecosystem-soil environments. Understanding how cycles of drought and extreme heat affect soil EAs under agroecosystems will provide valuable information regarding SOM dynamics and biogeochemical cycling that affect productivity.

Recognizing the record-setting drought and heat conditions occurring since the end of 2010, a soil sampling effort was initiated to better understand the effect of this extreme climatic event on EAs involved in C, N, P, and S cycling, along with SOM analysis, in agroecosystems. Our first objective was to determine the temporal response of EAs, beginning during peak drought conditions (July 2011) and continuing up to one year afterward. Our second objective was to evaluate if management history (i.e., rotation vs. monoculture cotton) could be differentiated via measurement of EAs during and after the drought on two different soil types (loam and sandy loam). Soil samples were collected from fields that had been under dryland monoculture cotton or cotton-forage rotation for at least five years. All fields were sampled during the peak of the drought/heat wave (July 2011) and when drought conditions improved slightly (March 2012), with only the loam fields sampled after one year (July 2012).

2. Materials and methods

2.1. Site descriptions

The SHP region has a dry steppe climate with mild winters and a mean annual precipitation of 465 mm (with most of the precipitation occurring from April through October). Two dryland production systems (monoculture cotton and a cotton-based rotation) on two soil types (loam and sandy loam) were selected and described in detail in Acosta-Martínez et al. (2011) and Davinic et al. (2013), respectively. The loam soil belongs to the Pullman series (Fine, mixed, thermic Torrertic Paleustolls) with an average pH of 7.4, 18.5% clay, 53.0% sand and 28.5% silt. These fields are located at the Texas Tech University field laboratory in New Deal, TX (33°45′N, 101°47′W; 993 m elevation). The sandy loam belongs to the Olton series (fine, mixed, superactive, thermic Aridic Paleustolls) with an average pH of 7.5, 12.0% clay, 69.5% sand and 18.5% silt. The fields are located at the USDA-ARS farm near New Deal, TX, USA (33°42′N, 101°49′W; 990 m elevation).

The monoculture system was tilled continuous cotton (*Gossypium hirsutum*) for both the loam and the sandy loam for at least five years prior to sampling. The rotation evaluated in both soils was tilled cotton rotated with a forage crop. The tilled cotton was rotated with forage sorghum (*Sorghum bicolor* L.) in the sandy loam for the last 5 years prior to this sampling. Similarly, tilled cotton was rotated with forage sorghum in 2004 and 2008 or foxtail millet (*Setaria italica* (L.) P. Beauv.) during other years in the loam (Zilverberg, 2012). Foxtail millet and forage sorghum are highly comparable C_4 forage crops with similar rooting structures and canopy features that require similar management practices involving tillage. Both are drought resistant, making them primary options to rotate with cotton in this semi-arid region.

2.2. Climatic conditions for each sampling time

Climate data was collected from the Lubbock National Weather Service weather station (NCDC, 2013), located within 10.5 km of all sample sites. Palmer drought severity indexes (PDSI) presented were calculated by the National Oceanic and Atmospheric Administration for the Texas Climate Division 1-High Plains and Panhandle region (NCDC, 2013), which encompasses most of Northwest Texas including the fields sampled. The PDSI is a soil moisture algorithm calibrated for relatively homogeneous regions, and a value below −4.0 is considered extreme drought conditions (Palmer, 1965). Soil temperature data was collected by the Texas Tech University West Texas Mesonet (WTM, 2013). The soil samples were taken from 0 to 10 cm during the peak drought/heat wave conditions (July 2011), after a reduction in the drought index was observed (March 2012), and after one year (July 2012) as summarized in Fig. 1. During July 2012 only the fields under loam soil were sampled as the fields under the sandy loam soil were converted to different cropping systems. Detailed discussion of climatic conditions for each sample time is below.

July 2011: Samples were taken on 25 July, and the average PDSI during this month was −6.1. Prior to this sampling, weather conditions were among the hottest and driest ever recorded for the SHP. During June and July 2011, average daily air temperature was 30.0 °C with an average daily maximum of 37.7 °C. These were the two warmest months on record in Lubbock, 5.7 °C and 3.6 °C above the monthly mean, respectively. Less than 2 mm of total precipitation occurred during these two months. In fact, the last precipitation event greater than 2 mm occurred in mid-May 2011, over 70 days prior to soil sampling. Overall mean soil temperature (5 cm) during June and July was 35.7 °C, the average daily maximum soil temperature was 45.0 °C, and the highest measured soil temperature was 48.0 °C. Gravimetric water content of soil samples was less than 2% for all soils at the time of sampling. Given the extreme weather conditions, it was not possible to establish crops, so all plots were fallow with bare soil during sampling.

March 2012: Despite precipitation during late 2011 and early 2012, less intense drought persisted with an average monthly PDSI of −3.3. Total precipitation was 18 mm during March, mean air temperature was 15.5 °C, and mean monthly soil temperature was 10.7 °C. A typical soil warming pattern occurred during the month,

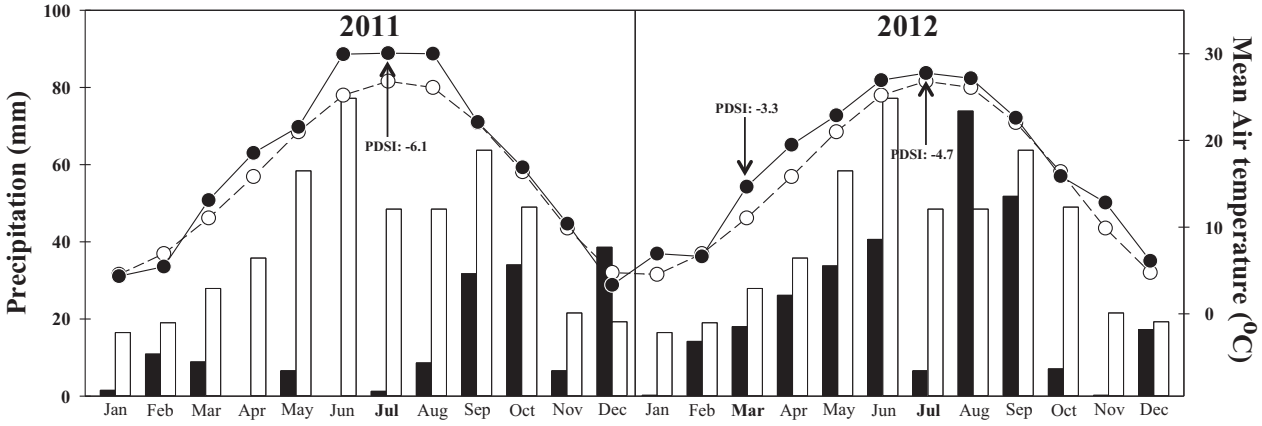

Fig. 1. Monthly total precipitation (filled bars) and mean temperature (filled circles connected by solid lines) during 2011 and 2012 relative to recent historical (1981–2010) monthly total precipitation (open bars) and mean temperature (open circles connected by dotted lines) in Lubbock, TX, USA. Average monthly Palmer drought severity index (PDSI) is given for each of the three sample times.

with mean temperatures increasing from 8.1 °C to 21.1 °C from the first to last week in March when sampling occurred (28 March). Approximately 14 mm of precipitation occurred one week prior to sampling, resulting in much higher moisture soil conditions than July 2011. Average gravimetric water content was greater for the rotation (11% and 9.8% in the loam and sandy loam, respectively) than for the monoculture (5.4% and 7.4% in the loam and sandy loam, respectively). As is a typical practice in this region, fields were under winter fallow during the time of sampling.

July 2012: Climatic conditions were still dry (PDSI was −4.7) with above average temperatures, but they were not as extreme as during July 2011. Mean air temperature was 27.8 °C, with an average daily maximum of 34.9 °C. Total precipitation was only 6.6 mm during July, but most of this occurred three days prior to sampling on 24 July, resulting in similar soil moisture content as those reported in March 2012. Mean soil temperature was 32.2 °C during July, with an average daily high of 40.4 °C. The average gravimetric water content of the loam soils was 11.5% under rotation and 3.8% under monoculture. Though crops were established in spring 2012, continuing drought conditions minimized growth so that only small, drought-withered cotton plants were present during sampling in the monoculture field only.

2.3. Selected soil properties including enzyme assays

Samples were sent to a private laboratory to determine soil pH (1:1 soil/water ratio), Mehlich-3 phosphorus, and total C and N (LECO TruSpec CN Analyzer, St. Joseph, MI) for all sampling times (Ward Labs, Kearney, NE). The activities of acid phosphatase, alkaline phosphatase, phosphodiesterase, arylsulfatase, α-galactosidase, β-glucosidase and β-glucosaminidase were assayed using field-moist soil (0.5 g oven-dry equivalent, <5 mm) with their appropriate substrate (p-nitrophenyl derivate) and incubated (37 °C) at their optimal pH following the assay conditions described in Tabatabai (1994) or Parham and Deng (2000). The EAs determined according to the release from p-nitrophenol as the reaction product were expressed in mg of p-nitrophenol released kg^{-1} soil h^{-1}. Three amidohydrolases (aspartase, urease, and L-asparaginase) were assayed using field-moist soil as also described in Tabatabai (1994). Briefly, steam distillation for the assay of amidohydrolases was performed using a Foss Kjeltec 2200 Auto Distillation Unit (FOSS North America, Eden Prairie, MN), and the distillate was titrated using a Mettler Toledo DL 50 titrator (Mettler-Toledo Inc., Columbus, OH). Results from amidohydrolases were expressed in NH_4^+-N released g^{-1} soil 2 h^{-1}. All EAs were assayed in duplicate with one control, to which substrate was added after incubation and subtracted from a sample value.

2.4. Statistical analyses

Both cropping management histories (monoculture cotton and the cotton-forage crop rotation) were represented within each soil type (loam and sandy loam). Ten composite samples were randomly-selected in each field and each composite sample was a mixture of three near locations. The soil samples were random samples from our four populations of inference and statistical inference is restricted to these four fields (Wester, 1992). The effect of sampling date was analyzed as a repeated measures factor in a linear mixed model that included fixed effects of soil type, management history, sampling date and all of their interactions. When interactions were significant, simple main effects were tested, followed by simple effect tests (Kirk et al., 1995). Residuals were tested for normality with Shapiro–Wilk (1965). Mean, standard error, and the heat map were calculated using R statistical software (ver. 2.14.0). To compare EAs across soil type, management history and sampling times, a supplemental heat map was used where color intensity reflects differences in EAs (i.e., darker colors reflecting higher values). This heat map shows also a percent of the difference of each enzyme activity between the rotation and monoculture for each soil type and sampling time.

3. Results and discussion

3.1. Comparison of soil EAs during and after the 2011 drought/heat wave

Although high temperatures and drought conditions are not rare in the SHP, the year 2011 was extraordinary with some of the warmest and driest conditions ever recorded (Hoerling et al., 2012), which had significant impacts on the soil metabolic functioning according to the ten enzymes evaluated over time. In general, eight out of the ten EAs (exceptions are arylsulfatase and asparaginase) were higher during the peak drought/heat wave conditions captured with the July 2011 sampling compared to less intense drought and temperatures eight months later (March 2012 sampling) (Figs. 2 and 3). There were six EAs showing a significant difference due to management history (monoculture and rotation) and/or sampling time (July 2011 and March 2012) independent of soil type ($P > 0.05$) (Fig. 2). Key enzymes involved in C (β-glucosidase, β-glucosaminidase) and P cycling (phosphodiesterase, acid and alkaline phosphatases) were significantly higher

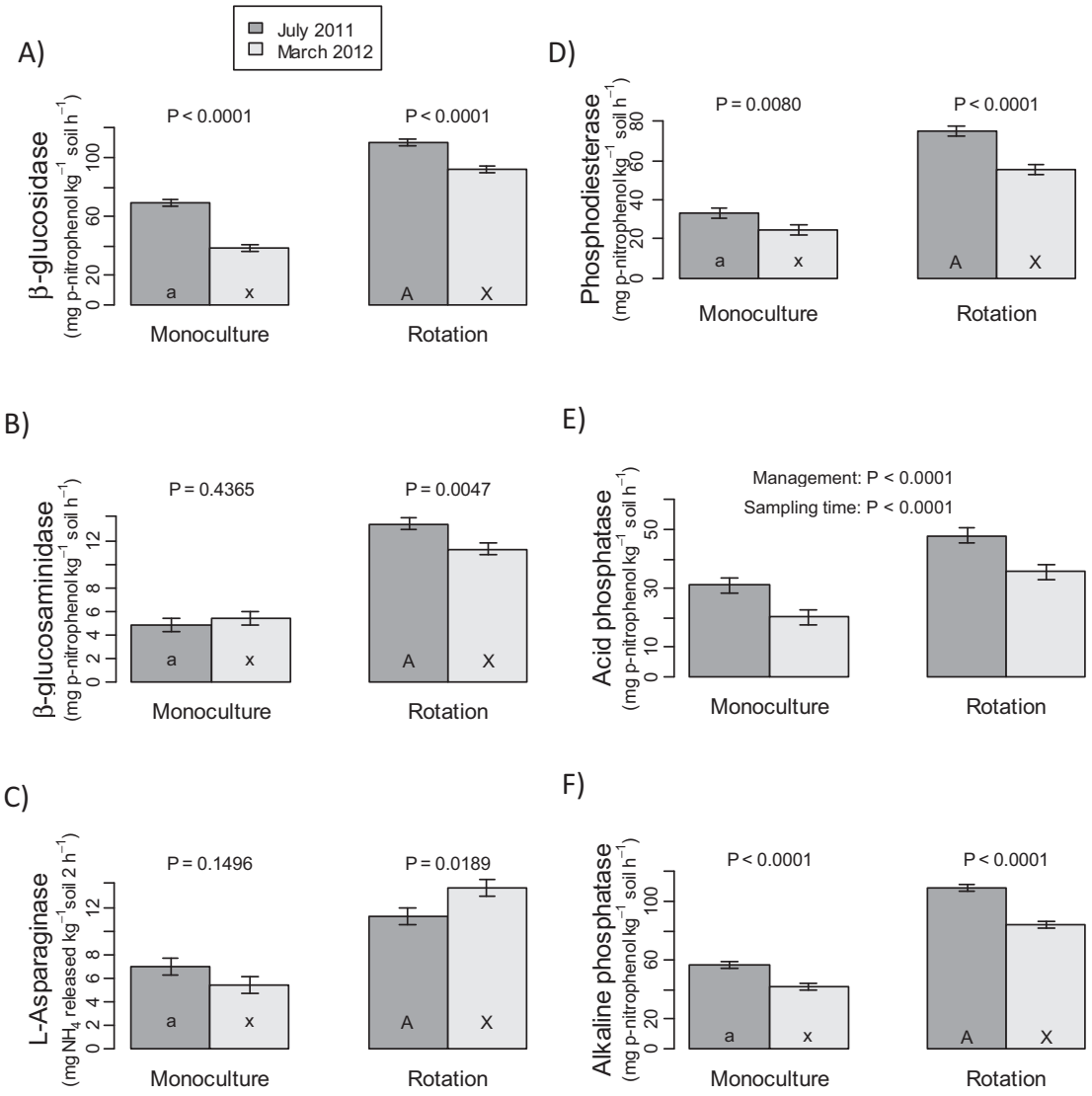

Fig. 2. Enzyme activities which showed a significant difference due to management history (monoculture and rotation) and/or sampling time (July 2011 and March 2012) independent of soil type (averaged across both soils, $P > 0.05$). For each enzyme, lower and upper case letters within each sampling date indicate differences due to management history ($P < 0.05$). P values above pairs of bars compare sampling dates within a management history.

(19–79%) in July 2011 than in March 2012. The response of the other four EAs (α-galactosidase, arylsulfatase, aspartase and urease) was not always consistent in both soils, as indicated by a significant three-way interaction between sampling time, soil type, and management history (Fig. 3). For example, aspartase activity was higher in July 2011 than March 2012, which was true for both soils and management, while α-galactosidase activity decreased significantly from July 2011 to March 2012 only in the sandy loam and urease activity decreased only in the rotation of the loam. Drought and heat waves often coincide; thus, while it was not possible to separate the effects of each component in our study, the natural occurrence provided a unique opportunity to compare with results obtained from soil manipulations under lab or field conditions.

Previous research has found that simulated drought conditions over longer time periods than addressed here will generally cause declines in potential EAs. For example, significant declines in EAs involved in C, N and P cycling were found after 5–6 years of simulated drought conditions using water exclusion in separate studies in a shrubland and an oak forest in the Mediterranean (Sardans and Peñuelas, 2005, 2010; Sardans et al., 2008a,b). Prolonged warming alone (5–6 years) resulted in increases (10–38%) in urease and β-glucosidase activities (Sardans et al., 2008a). Studies addressing early effects of warming and precipitation changes found little effect on potential EAs during the first year in fields under perennial grasses and forbs (Steinweg et al., 2013) and the Chihuahuan desert grassland (Bell et al., 2009). During our study, the loam soil was sampled three times (July 2011, March 2012, and July 2012), which allowed for a comparison a full year after the initial sampling during peak drought/heat wave conditions. Drought conditions persisted into July 2012 according to PDSI (−4.7), but conditions were less intense, with daily temperatures on average 2.2 °C lower than in July 2011, and gravimetric soil water content was 3.8–11.5% compared to <2% during July 2011. When comparing EAs over these three sampling times, six EAs showed a time by management interaction ($P < 0.05$) (Fig. 4). For this group of EAs, alkaline phosphatase and aspartase showed a continual decrease over time (July 2011 > March 2012 > July 2012) in both management histories, with urease showing the same decrease for the rotation (Fig. 4a–c). Although phosphodiesterase and β-glucosaminidase activities were generally highest in July 2011, these EAs did not continue to decline over all three sample times (Fig. 4d and e). The

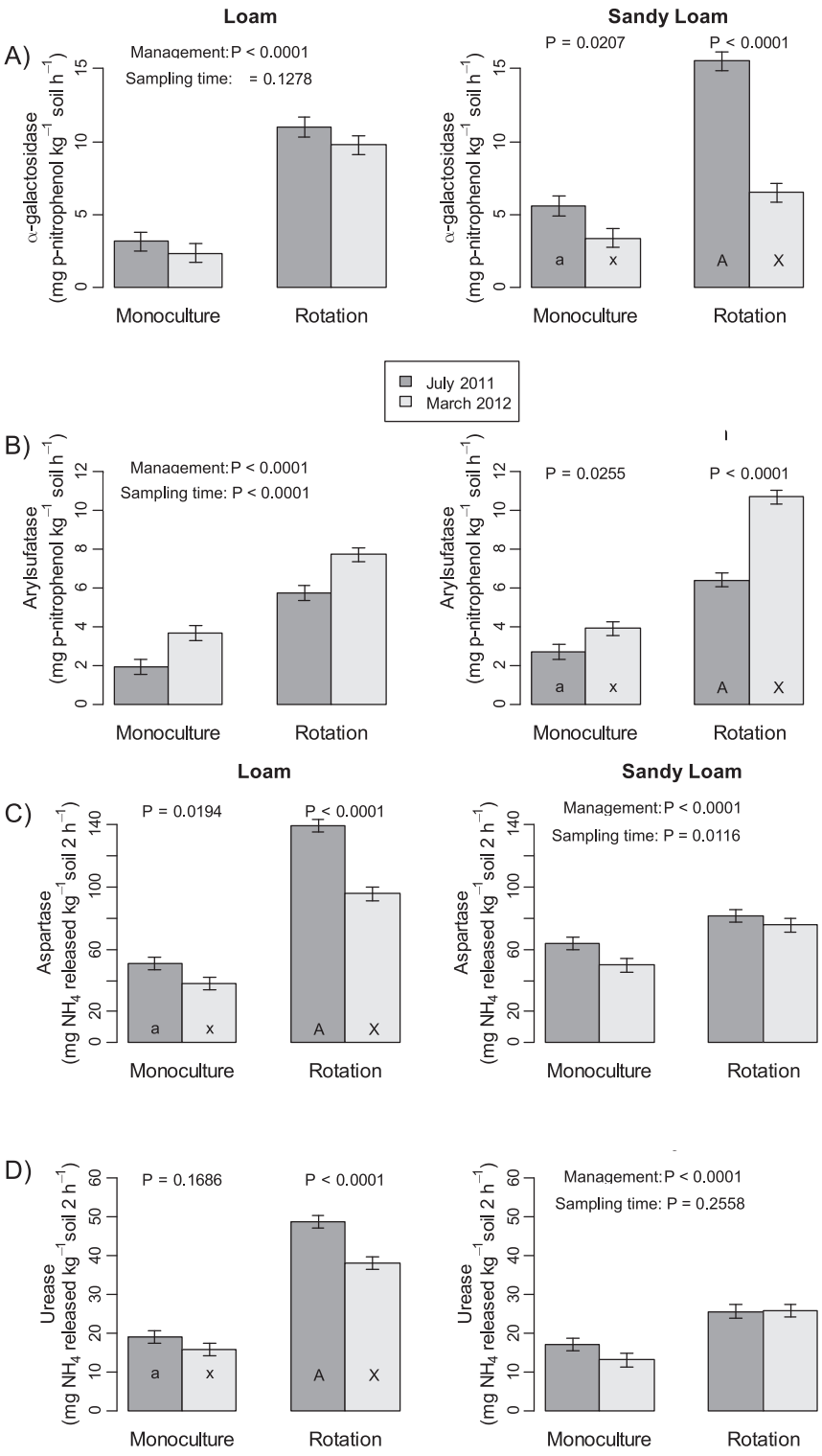

Fig. 3. Enzyme activities that were affected by a three-way interaction ($P < 0.05$) of management history (monoculture and rotation), soil type (loam and sandy loam), and sampling time (July 2011 and March 2012). Within an enzyme and soil type, absence of letters in bars indicates that management history and sampling time effects did not interact ($P > 0.05$); suspended P values are associated with tests of sampling time and management history effects. When management history and sampling time interacted within a soil type, lower and upper case letters within a given sampling date indicate that management history means differ ($P < 0.05$); P values suspended above pairs of bars indicate differences between sampling time within a management history.

other four EAs (acid phosphatase, α-galactosidase, arylsulfatase and β-glucosidase) did not show a sampling time by management interaction, which allowed for the comparison of these main effects independently (Fig. 5). Among these four enzymes, activities of acid phosphatase, α-galactosidase and β-glucosidase were higher in July 2011 than July 2012.

The higher EAs during the peak drought/heat wave period of 2011 may be explained by a change in enzyme pool distribution (Schimel et al., 2007) toward increased extracellular pools as a result of a combination of different mechanisms. For example, extracellular enzyme pools, previously protected within SOM–clay complexes, were likely exposed by disruption of soil aggregates

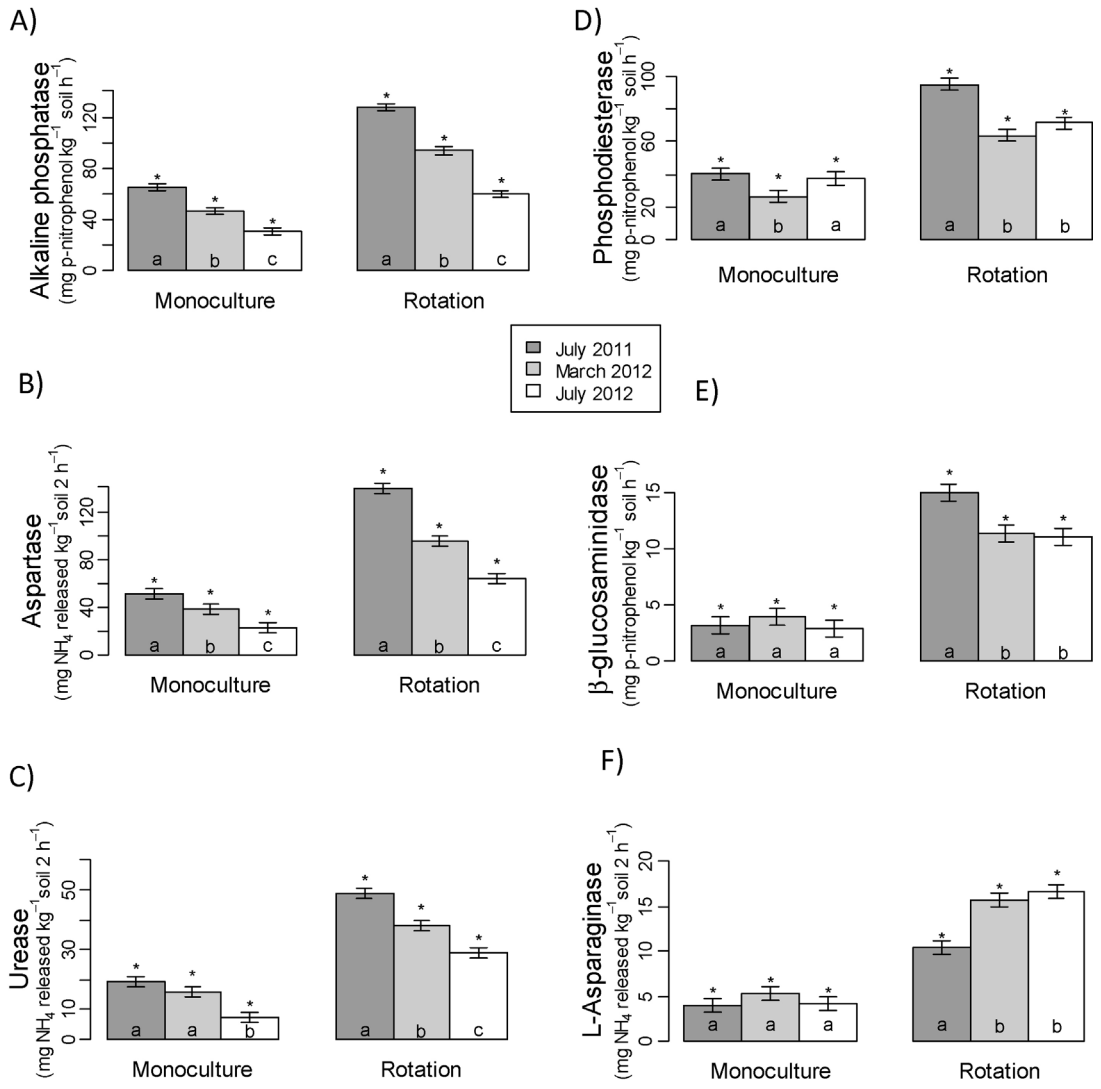

Fig. 4. Enzyme activities in the loam soil as affected by management history (monoculture and rotation) and sampling date (July 2011, March 2012 and July 2012). Management history and sampling time interacted ($P < 0.05$) for these enzyme activities; thus, sampling time means within a management history followed by the same lower case letter are not significantly different ($P > 0.05$); asterisks above bars indicate differences ($P < 0.05$) between management history means within a sampling time.

upon soil drying since there was <31 mm of precipitation in the ten months prior to our sampling. Another source of enzymes that may have supported the relatively high EAs we reported during peak drought may be via the release of enzymes upon cell death (Berard et al., 2011). Although the efficiency of extracellular enzymes increases with temperature (Koch et al., 2007), low moisture availability would likely limit enzyme and substrate diffusion (Allison, 2005; Bell et al., 2010). However, soil microorganisms may compensate for these stressors by increasing enzyme production (Harder and Dijkhuizen, 1983). Others have also hypothesized that in some cases microorganisms may produce small amounts of extracellular enzymes regardless of substrate availability, as a sensing mechanism to detect substrate (Klonowska et al., 2002; Wallenstein and Burns, 2011). It is possible that a portion of the extracellular enzyme pool would have been hydrolyzed by proteases, but perhaps the pool of proteases was not large or active enough (low turnover) to significantly reduce the relatively high enzyme pool measured during peak drought conditions in July 2011. It is important to acknowledge that thermal controls of extracellular enzymes are very complex and likely differ for each enzyme, season and region (Wallenstein and Burns, 2011). The soils in this study are located in a semi-arid environment which may pre-condition these enzymes to sustain or possibly even increase activity during drought and temperature stress.

Though we believe there was a shift toward a greater extracellular enzyme pool by July 2011, changes in microbial community composition may have also contributed to the higher EAs compared to the other sampling times. Studies on water manipulation alone (induced drought) have reported shifts in the microbial community (Berard et al., 2011). Drought induced a shift that favored fungal populations relative to bacterial populations (Bell et al., 2009) and warming treatments increased *Acidobacteria* and *Crenarchaeota* populations compared to control treatments (Sheik et al., 2011). We actually found the relative abundance of fungal orders *Dothideomycetes* and *Tremellomycetes* were approximately two times greater in July 2011 than in March 2012 in another study (Acosta-Martínez et al., Unpublished results). Additionally, we found a predominance of *Proteobacteria*, *Actinobacteria*, *Chloroflexi* and *Bacteroidetes* while lower *Acidobacteria*, *Verrucomicrobia* and *Gemmatimonadetes* in July 2011 compared to March 2012 for these soils. Our previous studies, especially in the loam, found correlations among some of these bacterial phyla, e.g., *Proteobacteria*,

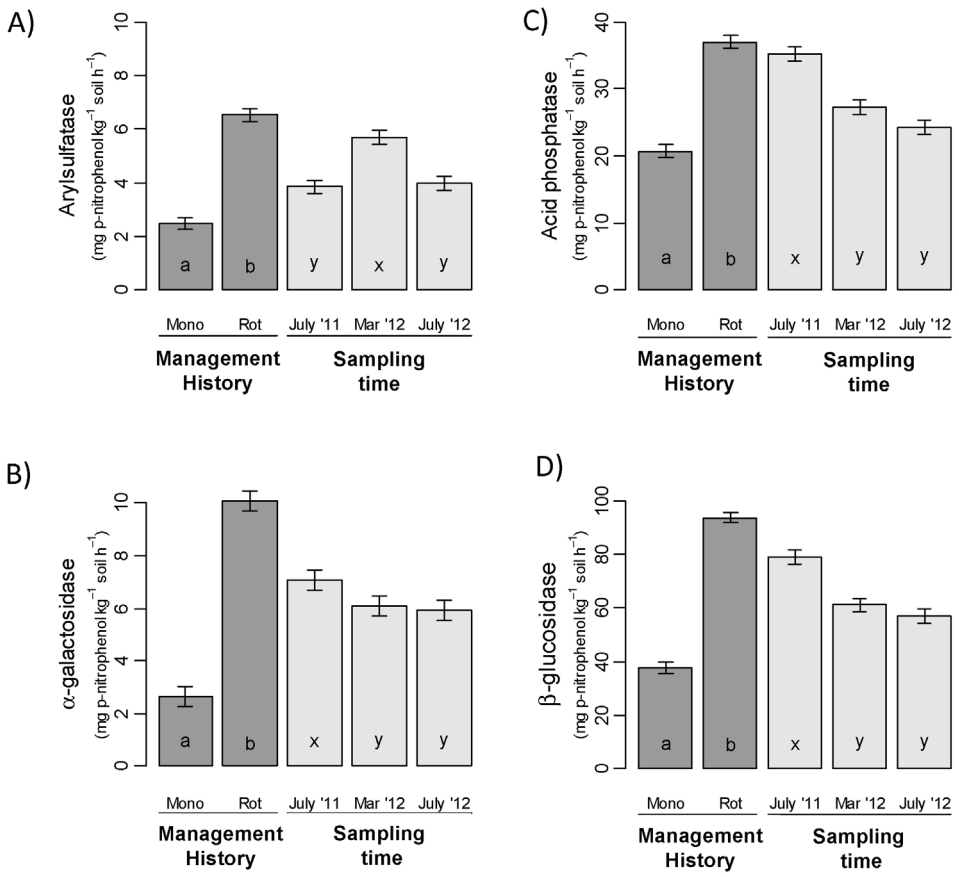

Fig. 5. Enzyme activities in the loam which showed no significant interaction ($P > 0.05$) between management history (monoculture and rotation) and sampling date (July 2011, March 2012 and July 2012), and thus, each main effect comparisons are shown independently. Management history means followed by different lower case letters 'a, b' are significantly different ($P < 0.05$), and sampling time means followed by different lower case letters 'x, y' are significantly different ($P < 0.05$).

and the EAs evaluated (Acosta-Martínez et al., 2010). Many members of the predominant bacterial communities we found during July 2011 have been reported to be tolerant to extreme conditions of dessication or gamma radiation (Singleton et al., 2003; Mongodin et al., 2006; Gardner et al., 2012) and may have been a significant source of the intracellular enzymatic pool and/or the extracellular enzymes that were better adapted to extreme conditions experienced during the study.

The mechanisms explaining the decline from July 2011 to July 2012 for these agroecosystems may differ from other ecosystems and soil conditions. Cotton crop residue from the 2010 growing season was still present on the soil surface during the July 2011 sampling, though cotton produces little biomass even compared to other crops grown in this semi-arid region (Acosta-Martínez et al., 2011). Since drought prevented crop establishment and resulted in no plant residue input during 2011, it is most likely that the continual decrease in many of the EAs could reflect an exhaustion of organic substrates/resources and perhaps gradual denaturation of the enzyme proteins. If the increased potential EAs during this drought/heat wave reflect actual conditions, it could also negatively impact the SOM content of these semi-arid soils. Though changes in total C are generally not detected during a short time frame, analysis of total C showed a significant reduction in the rotation from 7.5 to 6.2 and 6.3 to 5.8 g kg^{-1} soil from July 2011 to March 2012 in the loam and sandy loam, respectively (Table 1). Less significant change in total C occurred under monoculture after the drought, which is likely due to the combination of lower metabolic activity (i.e., lower EAs) and less labile C compared to the rotation. The decline in SOM observed suggests that more frequent and extreme droughts could substantially reduce the already low organic matter and affect the long-term sustainability of these soils.

By addressing multiple enzyme-mediated reactions transforming different nutrients, our study revealed the possibility that EAs could respond differently to climate change on these agroecosystems. For example, arylsulfatase and asparaginase activities responded to the drought/heat wave in a different manner than the other EAs indicating the possibility of different origin and location of these enzymes. Arylsulfatase activity increased 34–95% from July 2011 to March 2012 in both soils (Fig 3b). Additionally, this enzyme activity reached similar levels in July 2012 to the levels found in July 2011 (Fig. 5a). Asparaginase activity increased under the rotation for both soils after July 2011 (Figs. 2c and 4f). Previous work on arylsulfatase activity support that this increase may be due to a more predominant intracellular pool for this enzyme (Ndiaye et al., 2000; Klose and Tabatabai, 2000), which represented up to 78% of the total activity in similar soils from this region (Acosta-Martínez et al., 2004a,b). When soil moisture/temperature conditions improved in March 2012, it is likely that microbial communities increased and contributed to the increased activity of this enzyme. This may also explain the increase seen in asparaginase activity, though there is less research on this enzyme. If these two EAs (especially arylsulfatase) are in fact, tightly linked to active microbial communities, this further supports our hypothesis of a shift toward greater extracellular pools during the drought for the other EAs measured here. Additionally, the different response of arylsulfatase activity suggests that S mineralization is more tightly linked to active microbial communities whose size fluctuates highly due to drought in these soils.

Table 1
Selected soil chemical properties as affected by soil type and cropping system history. Mean and standard error (in parenthesis) are shown.

Soil type/cropping system	Sampling time	Total C (g kg^{-1} soil)	Total N (g kg^{-1} soil)	NO_3-N (mg kg^{-1} soil)	P (mg kg^{-1} soil)	K (mg kg^{-1} soil)	pH
Sandy loam							
Monoculture	July 2011	4.2 (0.24)	0.45 (0.022)	13 (0.6)	55 (3.7)	359 (7)	7.2 (0.02)
Rotation		6.3 (0.32)	0.62 (0.036)	17 (1.3)	46 (1.1)	525 (15)	7.5 (0.04)
Monoculture	March 2012	4.1 (0.11)	0.41 (0.012)	13 (1.6)	36 (0.8)	336 (5)	7.0 (0.06)
Rotation		5.8 (0.18)	0.57 (0.017)	20 (1.8)	35 (5.7)	452 (20)	7.3 (0.05)
Loam							
Monoculture	July 2011	4.5 (0.14)	0.41 (0.024)	6.2 (0.43)	16 (1.2)	364 (10)	8.1 (0.02)
Rotation		7.5 (0.15)	0.74 (0.024)	31.6 (2.19)	55 (0.8)	633 (10)	7.3 (0.02)
Monoculture	March 2012	4.4 (0.12)	0.45 (0.019)	3.4 (0.29)	22 (1.3)	374 (12)	8.2 (0.02)
Rotation		6.3 (0.14)	0.66 (0.017)	17.4 (0.92)	38 (2.5)	508 (13)	7.6 (0.06)
Monoculture	July 2012	4.0 (0.07)	0.43 (0.009)	10.6 (0.68)	24 (1.0)	357 (5)	8.2 (0.02)
Rotation		6.2 (0.17)	0.67 (0.015)	28.9 (1.73)	55 (1.1)	569 (13)	7.5 (0.05)

Monoculture is a continuous cotton system; rotation is sorghum–cotton (sandy loam) or millet–cotton (loam).

3.2. EAs as affected by management during the extreme drought and heat wave

Previous work had detected a significant difference in EAs between the two management histories (Acosta-Martínez et al., 2011). Given the extremity of the 2010–2011 drought/heat wave, we hypothesized that the influence of management history would be decoupled from EAs. Our results, however, did not support this hypothesis. In general, the EAs continued to be a fingerprint of the soil management history as the majority of EAs were higher in the rotation compared to monoculture in both soil types in July 2011 (Figs. 2 and 3) as well as in July 2012 for the loam (Figs. 4 and 5). Although these soils only have about 1% organic matter content, these findings demonstrate that an increase in C content under rotations compared to cotton monoculture ($P < 0.05$, Table 1) could have helped to protect enzymes from denaturation or protease hydrolysis during the drought/heat wave.

The degree to which EAs responded to the management history differed depending on the soil type. In general, the EAs were 55–373% higher under rotation than in the monoculture in the loam compared to 23–176% in the sandy loam (Fig. 1S). However, EA differences due to management history for all P cycling enzymes were similar for both soil types. The phosphatases, which are crucial in organic P transformation, are sometimes more dependent on changes in soil pH than organic matter content or levels of disturbance (Acosta-Martínez et al., 2004a). Regardless, our results highlight the ability of soil EAs to serve as fingerprints of soil management despite extreme-record drought conditions.

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The frequency and intensity of drought in Texas are predicted to increase in response to climate change (Overpeck and Udall, 2010; Strzepek et al., 2010). Ecosystem responses to these events may be dependent upon management history and land use. For example, annual cropping systems may be less resistant to these stressors in comparison to perennial vegetated systems where biomass inputs, root secretions, and soil coverage may protect ecosystem functionality. Our study, to our knowledge, provides the first evidence that variables such as the management history and soil type are important drivers of ecosystem resilience and resistance under extreme weather conditions. The combination of soil type and climate zone could play a significant role on the response to a drought in the enzymatic pool responding to extreme weather events. For example, although some humid soils support relatively equal distributions of intracellular and extracellular enzymes (Klose and Tabatabai, 2000), extracellular enzyme pools may dominate in semi-arid, drought-prone agricultural soils, which will impact the kinetics, stoichiometry and breakdown/turnover of the enzymes. It will therefore, be important to continue evaluating the microbial responses and the enzymatic capacity of soil especially in agroecosystems under diverse management histories, climatic zones and soil types.

4. Conclusions

This study was the first to explore the effects of a natural drought and heat wave on soil EAs critical in biogeochemical cycling in agroecosystems. These agroecosystems supported a high level of functional redundancy (i.e., enzymatic activity); the majority of EAs involved in C, N and P biogeochemical cycling were greatest in July 2011 during the peak of this extreme event whereas only two out of the ten EAs measured (e.g., arylsulfatase and asparaginase activities) were lower in July 2011 than in March 2012 under reduced soil moisture and temperature stress. The higher EAs maintained in fields managed as a crop rotation compared to monoculture cotton reflects the importance of conservative management in building a resilient extracellular enzymatic pool to sustain soils metabolic capacity under extreme adverse climatic conditions. Despite this increased potential resilience, sustaining high metabolic capacity in low organic matter soils under recurrent droughts and heat waves may deplete organic matter reserves and ultimately reduce the ability of the ecosystem to recover. Given current projections of increased frequency and intensity of drought and heat in this and similar semi-arid regions, understanding how drought and heat wave cycles affect EAs will provide critical information to better predict soil organic matter dynamics, nutrient transformations, and overall agroecosystem resiliency and resistance to climate change.

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Soil Type	Management History	Sampling Times	β-glucosidase	α-galactosidase	β-glucosa minidase	Alkaline phosphatase	Acid phosphatase	Phospho diesterase	Arylsulfatase	Urease	Asparaginase	Aspartase
LOAM	Rotation	July 2011										
	Monoculture		95%	246%	373%	97%	55%	137%	197%	156%	159%	174%
	Rotation	March 2012										
	Monoculture		191%	313%	188%	102%	89%	143%	109%	141%	201%	151%
	Rotation	July 2012										
	Monoculture		202%	301%	280%	97%	106%	91%	235%	286%	296%	189%
SANDY LOAM	Rotation	July 2011										
	Monoculture		35%	176%	84%	82%	53%	111%	138%	50%	23%	28%
	Rotation	March 2012										
	Monoculture		102%	91%	64%	96%	63%	108%	173%	97%	104%	52%

Figure- supplementary